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Cognition in Plants

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13.1 Abstract

We discuss the possibility and the meaning of the claim that plants are cognitive from the perspective of *Embodied Cognition*. In *Embodied Cognition*, the notion of cognition can be interpreted very broad and applies to many free-moving creatures. In this chapter, we discuss whether and, if so, how this approach applies to intelligence in plants. Building on work from 'plant neurobiology,' we discuss the differences in speed between plants and animals, similarities between sensory-driven plant growth and animal memory, and the presence of offline behavior in plants. In our view, these examples show that under a wide, embodied interpretation of cognition, plants may well qualify as representatives.

13.2 Introduction

Plants exhibit much more complex and flexible adaptive behavior than most people would expect (Trewavas 2003). With that being said, the very possibility of plant behavior as exhibiting certain cognitive aspects strikes many people as outrageous, whether they are plant scientists or not. In this chapter, we will discuss the possibility and meaning of claiming that plants might be cognitive by turning to current discussions within the field of embodied and embedded cognition ('*Embodied Cognition*', hereafter) and its links to biology. In this context, the notion of cognition is drawn around perception-action phenomena and its nature applies much wider than human-level thought.

Embodied Cognition takes perception-action as its major focus, and within this embodied perspective, most animal and even bacterial behavior can be considered cognitive in a limited form. *Embodied Cognition* stresses the fact that free-moving creatures are not simple, hard-wired reflex automatons but incorporate flexible and adaptive means to organize their behavior in coherent ways. Even when it may go too far to ascribe a mind to such systems, they deserve an acknowledgement of the intelligence involved in the things they do, and for this reason, the notion of cognition seems appropriate.[1] So far, the notion of cognition has not been extended to plants. One reason is simply that most cognitive scientists, even those involved in *Embodied Cognition*, are simply unaware of what plants can do. This is simply remedied. However, a theoretically more important reason to exclude plants from the wider cognitive domain sketched by *Embodied Cognition* seems to be the lack of the kind of

[1] It is thus important to differentiate here between this wide interpretation of *cognition*, which may apply in a meaningful way far beyond the human case, and the notion of *mind*, which may well remain highly restrictive and possibly limited to human beings.

sensorimotor organization that is the major focus of embodied cognition. We will focus on this issue.

In recent years, the issue of plant intelligence or cognition and even 'plant neurobiology' has become a lively debate among plant scientists (e.g. Alpi et al. 2007; Barlow, 2008; Firn 2004; Trewavas 2003, 2005; see also Calvo 2007, and references therein). So far, this debate has gone unheeded within *Embodied Cognition*, nor has this debate itself relied on ideas from *Embodied Cognition*. We think the discussions in the plant sciences can benefit from work in *Embodied Cognition*, which has already done significant progress on clarifying the notion of cognition and possible criteria for its use. At the same time, confronting *Embodied Cognition* with the 'plant question' is sure to raise important new inputs in the field of *Embodied Cognition* itself.

In this chapter, we will discuss the question whether an extended reading of cognition, as developed within *Embodied Cognition* might apply to plants. Within *Embodied Cognition*, the notion of cognition – being based on perception and action – is used to make sense of a wide range of behaviors exhibited by 'simple' animals, like nematodes or flies. The message is clearly that we should set generalizing dismissive intuitions concerning such animals aside and go for a more empirically informed approach. We believe that this open attitude is also beneficial to the study of possible cognitive phenomena in plants.

The chapter has the following structure. In section 3, we introduce the discussion on what cognition is, and sketch the difficulties in clarifying this key notion for the cognitive sciences. In section 4, we formulate a wide reading of cognition as derived within *Embodied Cognition*, also taking in biological considerations. This wide reading is subsequently condensed into five constraints on cognition, two of which explicitly highlight the need for an animal-like sensorimotor organization. In section 5, using the work of Hans Jonas, we discuss *why* having a sensorimotor organization is important for cognitive phenomena and whether plants may fulfill some of these functions in alternative ways. In the next three sections, we discuss plant research findings from which we conclude that, in this light, plants can fulfill these constraints to a significant degree. We introduce the main tenets of plant neurobiology in section 6 and argue that the differences in speed and form of plant behavior do not exclude a cognitive interpretation. In section 7, we argue for the similarities between plant growth and animal memory. Section 8 deals with plant control structures for forms of offline cognition. We conclude that these examples show that plants can be considered to be minimally cognitive and to constitute an important domain for cognitive studies.

13.3 What is cognition?

What is cognition? Although cognition is one of the core concepts in the behavioral and cognitive sciences, there is no generally accepted answer. For example, in his classic book *Cognitive Psychology*, Ulrich Neisser defined cognition as: "all processes by which the sensory input is transformed, reduced, elaborated, stored, recovered, and used." (1967, p.4) But this definition seems to include many artifacts, like tape recorders, and organisms, like plants, that were not intended to be labeled as cognitive. The classical cognitive sciences that grew up under the influence of people like Neisser used a much more limited interpretation of cognition: not all forms or information processing did suffice. The implicit extra constraint in this definition was that cognition involves the kind of information processing that also occurs in *human intelligence*, where it is described in terms like perception, planning, thinking and action.

Because this field was intrinsically interested in the human mind and not in any other topic, this implicit limitation worked quite well in practice. No one had to provide an answer why tape recorders and plants were out, as these were not part of the topic studied. The notion of cognition itself became widely interpreted as referring to the information processing mechanisms that describe how the human mind operates. Human cognition became the default

interpretation of cognition and also the yardstick by which the cognitive abilities of other animals were to be measured. From that perspective, cognition is tantamount to characteristically human-like capabilities such as reasoning, problem-solving and symbolization. These processes have to be present to a significant degree before one can speak of a *bona fide* cognizer (Gould and Gould 1998). Internal, representation-handling processes are considered to be the source of these particular thinking skills. It is a matter of painstaking research to establish whether, and if so, which other creatures also exhibit these refined capabilities (see for example Heinrich 2000; Smirnova et al. 2003). In the human-based interpretation of cognition, organisms whose behavior does not unequivocally involve human-style-reasoning subsequently remain outside the cognitive domain. Cognition is a scarce commodity in this view.

Having an interest in *human* cognition, and not in the rest, is a way of carving up the domain that leaves little motivation for articulating what falls outside this domain. In the cognitive sciences, the behavior of nonhuman organisms receives comparatively little attention (for a notable exception, see Bekoff et al. 2002). Such behavior is often argued to be predominantly composed of inflexible, hard-wired reactions to environmental stimuli (e.g. Dennett 1984, 1996; Gould and Gould 1998; Sterelny 2001). As a result such behaviors are not considered as being very interesting from a cognitive perspective and only require closer attention when they come nearer to the human forms of intelligence (see also Godfrey-Smith 1996, 2001; Shettleworth 1998). Dennett (1984) and Hofstadter (1985), for example, talk about "sphexisms" in this context, drawing the term from an anecdote in which a digger wasp of the *Sphex* genus was manipulated so that it remained stuck in an iterative, automatic behavioral loop; endlessly repeating its own inbuilt, behavioral responses.[2] In other words, anthropocentric interpretations of cognition depict a rough dichotomy between intelligent cognizers, and inflexible, mechanic-like organisms merely capable of reflexive/instinctive behaviors.

However, there are important practical and theoretical problems with such a general dichotomy between human cognition and 'non-cognitive' inflexible, mechanistic behavior, as well as with a human-based interpretation of cognition. First, this putative dichotomy does not stroke with the underlying intricacies that make so-called 'non-cognitive' organisms tick, as it simply fails to provide a realistic account of the behavioral complexities that can be found in non-human organisms (Brooks 1999; Keijzer 2001; Roth and Wullimann 2001). When investigated in their own right, the mechanisms and processes required to generate these presumably non-cognitive behaviors are found to be very complex and extraordinarily difficult to replicate in robots (Prescott et al. 1999).

Second, the dichotomy does not cope with any differentiation within the so-called non-cognitive organisms. There are huge gaps between the behavioral capabilities of, for instance, nematodes and octopi, or between sharks and squirrel monkeys, all of which are - definitely to plausibly - considered 'non-cognitive' from an anthropocentric perspective. The assumption that the behavior of these 'lower' organisms is entirely composed of reflexes, instincts and/or hardwired reactions does not help to articulate how such very different behavioral capabilities come about.

Third, when one turns to the basic processes of cognition, and leaves aside their anthropocentric interpretation, it is clear that these processes, such as perception, memory, and action are dispersed extremely widely across and even beyond the animal kingdom. It is now even plausibly defended that these exemplar features of cognition are already present in invertebrates (Carruthers 2004; Keijzer 2001), and prokaryotic bacteria (di Primio et al. 2000; Greenspan and van Swinderen 2004; Lengeler et al. 2000; Müller et al. 2001).

Fourth, a general dichotomy makes it more difficult to develop a gradualist and diversified evolutionary account of how basic forms of cognition developed into different and more complex

[2] The story is actually a mere anecdote and not systematically corroborated by evidence (Keijzer, 2001)

ones. As it places the boundaries of cognition very high, say primates or, possibly, tool-users, the relevance of preceding evolutionary stages of intelligent behavior is blurred. The differences are stressed rather than possible continuities discovered.

All these considerations were known for a long time but did not have much impact within the cognitive sciences until the rise of *Embodied Cognition*. This new field of cognitive sciences came to the fore in the late eighties and the nineties as a reaction to the strong focus on explicit, reflective human thought. Hurley baptized this view 'the sandwich model' as it interpreted cognition as a separate inner filling, wedged between perceptual input and behavioral output (Hurley, 1998). *Embodied Cognition*, instead, stressed the ongoing, dynamic interactions between an agent and its environment by means of perception and action. In this view, perception-action processes became the starting point for intelligence, and complex human thought one of its offshoots.[3] Perception-action – and the sensorimotor organization it requires – thus becomes the online key feature of cognition, which is evolutionary expanded in higher-level cognizers to include all sorts of offline processing that exhibits representational characteristics.

One important consequence of *Embodied Cognition* was that the notion of cognition itself started to shift away from its human anchor. Roboticists, for example, started to make insect-like robots that had little to do with human cognition, but a lot with investigating a bottom up interpretation of intelligence, and thus a kind of cognition. In this context, the link to the human case became insufficient, leading for a call to formulate a *mark of the cognitive* (Adams and Aizawa 2001). How such a mark could be given remains a problem, but there seems to be a strong consensus that cognition involves processes such as perception, thinking, memory, and action. As already stressed, it is useful to differentiate between mind and cognition here, even though the two are often used intermingled within the cognitive sciences. While 'mind' may or may not remain closely tied to humans and in particular to consciousness, 'cognition' need not be intrinsically connected to either humans or consciousness. Thus while 'cognition' is a concept that can be stretched beyond its original use, this can be done without additional claims that all cognitive systems are to be seen as mindful in a way that is similar to human minds.

We think that the notion of cognition ought and can be developed in new ways to fill in the gap between the mindful and the mindless, and turn it into a gradient from human intelligence to inanimate nature. Godfrey-Smith (2001, p. 234) argued that cognition in the first place evolved to enable organisms to control their own behavior, allowing them to cope with environmental complexity. In his view, cognition "shades off" into basic biological processes such as metabolism. We believe that a proper interpretation of cognition should aim to become more specific about this "shading off", and allow for a better differentiation within the wide array of cognitive capabilities that are found in nature. In the next section, we will develop the outlines of a wide interpretation of cognition, as it can be derived from ongoing theoretical developments within embodied and biological views on cognition.

13.4 A biological and embodied perspective on cognition

Since *Embodied Cognition* provides the intrinsic connection between humans and cognition, work has begun to provide a more systematic account of cognition. Taking in artificial systems like robots makes this task very difficult and possibly impossible. For example, it is hard to make sense of the question whether a bacterium is as intelligent as a washing machine (Firn, 2004), because it is utterly unclear on which aspects of both one should focus. However, restricting oneself to naturally occurring, *biological* systems provides more grip (e.g. Barandiaran 2008; Keijzer 2001, 2003, 2006; Lyon 2006a, 2006b; Moreno and Etxeberria 2005; Moreno et al. 1997; Van Duijn et al. 2006). The main idea here is that cognition is (or originated as) a

[3] For introductions and overviews of Embodied Cognition, see e.g. Calvo and Gomila (2008), Clark (1997), Pfeifer and Scheier (1999), or Varela, Thompson, and Rosch (1991).

biological phenomenon and is used to manipulate the environment in ways that systematically benefit the living organization that exhibits these cognitive aspects. In this context, the question concerning minimal cognition is important (Beer, 2003): What is the minimal biological system to which the notion of cognition applies?

We will disregard claims that make life itself a form of cognition, but it can be argued that bacteria already provide examples of cognition (di Primio et al. 2000; Lengeler et al. 2000; Lyon 2006a; Van Duijn et al. 2006). Consider chemotaxis in *E. coli*. These free-moving bacteria use flagella to move around and can travel up or down gradients of several substances that they can ingest or need to avoid. All the basic ingredients for a minimal form of cognition are already present here, and discussing them will provide a suitable framework when it comes to judging the possibility of plant cognition.

As a living organism, *E. coli* involves a metabolic biochemical organization, which provides the fundamental energetic and constitutive processes of the bacterium, as it does for all living organisms. To stay alive, the bacterium needs substances that it can incorporate into its structures and it needs energy to drive these biochemical processes. This metabolic organization provides a basic form of normativity (Bickhard 2008) – differentiating '*bad for me from good for me*' – and can itself have adaptive characteristics. For example, a well-known form of metabolic adaptation is the 'lac operon' system, which regulates the metabolism of lactose in *E. coli*. This cluster of genes is normally dormant, because the bacterium predominantly metabolizes glucose. However, when the bacterium detects that glucose levels are very low and lactose is abundantly present in the environment, the lac operon system becomes dis-inhibited, subsequently allowing the transcription and expression of genes that enable lactose metabolism (Todar 2004). This form of metabolic adaptation is induced by environmental conditions, but still is a part of the organism's metabolic organization. The process consists of a change in the set of chemical reactions that together constitute the bacterium's metabolism.

Chemotaxis, on the other hand, is a different kind of process. It is itself not constituted by chemical reactions, but by physical changes in the position of the bacterium with respect to its environment. In other words, the bacterium interacts with its environment at the larger, physical scale of the *dispersion* of metabolically relevant substances. There are potential metabolic benefits to this interaction, but this manipulation of the environment—moving towards a food source, for example—is itself not a metabolic process. With respect to metabolism, chemotaxis is a second-order process, which is relevant for changing metabolic opportunities, and in this way expanding the adaptive opportunities of organisms to a considerable degree.

Manipulating the environment at larger scales to enable or enhance metabolic functioning is a very general biological strategy. Sponges pumping water through their bodies, plants growing leaves oriented toward the light, lions stalking their prey, and even humans discussing which restaurant to go to can be considered as examples. Why would all of these activities be cognitive? In the *Embodied Cognition* literature there is a clear intuitive cut off point, which limits cognition to systems showing a form of sensorimotor coordination. Cognition applies to free-moving agents, capable of reversible movements and perception. In this view, bacterial chemotaxis is a possible example of minimal cognition as it uses sensorimotor coordination to expand metabolic forms of adaptation and, in this way, provides a basic example of an organization that is also present in human cognition. Plants, fungi and sessile animals, however, would be left out of the cognitive domain insofar as they (seem to) lack this additional requirement.

Setting up an adequate sensorimotor organization requires a particular physical embodiment of an organism, be it bacterium or monkey. For bacteria, this comes in the form of specific chemical receptors such as methyl-accepting proteins, and actuators such as flagella or pili that enable the bacterium to move about (Berg 2000). It also involves a control system that enables the organism to initiate motion and use the perceptual feedback it generates to guide this motion. Within *Embodied Cognition*, it is customary to differentiate between online processing that is

under direct perceptual control, and offline processing which is to some extent decoupled from immediate perception-action. Online processing is cast as more basic, while offline processing is thought to be involved in more complex cognitive tasks, like those relating to memory or planning.

Importantly, E. coli already shows some offline capacities. It does not measure a concentration gradient by calculating the simultaneous difference between different sensors at different body-parts. Instead, *E. coli*, and many other bacteria, uses a TCST-system which acts as a memory and inner connection between sensors and effectors in a way that is functionally similar to the nervous system in multicellular animals. The TCST-system allows it to take sequential measurements of the substance concentration. When the bacterium happens to travel down the gradient, according to this memory, it tends to change directions randomly, and when it travels up the gradient, *E. coli* tends to maintain its course. The net result is a systematic form of chemotaxis.

Finally, in this biological and embodied perspective on cognition, the sensorimotor organization does not consist of simple and hard-wired behavior. All animal behavior results from a complex non-linear dynamical process involving a nervous system, a body and an environment that interact with one another on a continuous basis (Beer 1995, 2000; Keijzer 2001). Even seemingly repetitive and automatic behavior is still the result of complex non-linear processes, which show up when the larger behavioral repertoire of the organisms is taken into account. This also applies to our example of *E. coli*. We want to stress that the system's chemotaxis is actually much more complex than suggested so far, as it also adapts to the absolute concentration level of the substances, works in conjunction with sensitivity to several other substances, and is in itself part of a very flexible organization for behavioral control (Lyon 2006a). Merleau Ponty (1963) provided a clear and detailed analysis of how the seeming simplicity of environmentally controlled stimulus-response behavior results very easily as a methodological artifact when one tries to isolate a specific aspect of behavior from ordinary behavior of an animal.

To summarize, casting biological forms of sensorimotor coordination as the minimal form of cognition provides a clear and transparent starting point for thinking about cognition. In our view, by framing the issue of the nature of cognition from within the field of *Embodied Cognition* the question concerning plant intelligence can be suitably addressed. The problem to be solved first, however, is whether plants are not to be excluded from the cognitive domain as envisioned within *Embodied Cognition*.

13. 5 *Embodied Cognition* and plants

An embodied and biological perspective introduces a more open-ended interpretation of cognition and intelligence. The upshot of this enterprise can be summarized in five different constraints that apply to cognition as conceived in this way:

1. Metabolism provides a basic form of biochemical normativity for cognition.
2. Cognition proper (initially) consists of exploiting the spatio-temporal dispersal characteristics of metabolically relevant environmental features by movement of the organism.
3. This movement takes the form of various sensorimotor organizations.
4. A basic, online, sensorimotor organization can be expanded by using offline control structures that can, but need not, involve a nervous system.
5. Such a sensorimotor-based cognitive organization is a globally organized cohering unit, not a collection of individual stimulus-response relations.

The question to ask now is whether and, if so, how does this set of constraints apply to plants? To begin with, we must stress that the application of the first two constraints is not disputed. Plants metabolize, of course, giving them a basic motivational setup for doing things. There is no doubt either that plants manipulate their environment in a second-order way such that their

metabolic functions profit from this manipulation. Growing roots downward and light-catching parts upward suffice in this respect (Keijzer 2001).

The real rub for minimal cognition in plants comes from constraints 3 to 5. Constraint 3 imposes being *free-moving*, having a sensorimotor organization, as a requirement for cognition. It is here that the option of plant cognition seems highly problematical within an embodied perspective. However, adhering to being free-moving as an *intuitive* criterion is unsatisfactory. Within the biological domain, free-moving organisms may stand out as potentially intelligent beings, but why should we trust these intuitions? The question should rather be: Why would we consider being free-moving so important?

Up to now, plants have not received much attention within *Embodied Cognition*. Most of the field worked with a default assumption that intelligence was at a minimum an animal thing that was best caught in studies with free-moving agents such as robots, while excluding sessile plants. However, Hans Jonas (1966, 1968), now receiving renewed attention as an important thinker on the connections between biology and mind (Barandiaran 2008; Di Paolo 2005; Keijzer 2006), did take plants into consideration. Jonas tried to articulate the differences between plants, animals and humans in a way that highlights the relevance of being free-moving. In his view, the capacity for free movement is a key feature that is required for the development of intelligence as exhibited by animals, and a precondition for the evolution of human thought. Jonas' work can be used to argue that there exist fundamental differences between intelligence in plants and animals (e.g. Barandiaran 2008). At the same time, by clarifying in what way being free-moving is so important, he provides a clearer target to be challenged on empirical and theoretical grounds. Plants may very well fulfill these constraints, without moving about like animals do.

Jonas provides an analysis why motility, and in its wake sensing and emotion are key features when it comes to cognition. 4 He argues that animal motion is more than an intensified case of vegetative motion from which it differs in a number of physical respects: "in speed and spatial scale; in being occasional instead of continual; variable instead of predefined; reversible instead of irreversible." (Jonas 1968, p. 248). These criteria are important to make the difference between being free-moving – which plants are not, generally speaking – and having self-induced motility – which is present in plants. Jonas uses these physical differences as a foundation for a further argument that animal motion leads to a principled new way of coordination with the geometry of environmental space (1966, see also Barandiaran, 2008). Jonas makes the point as follows:

> Now it is the main characteristic of *animal* evolution as distinct from plant life that *space*, as the dimension of dependence, is progressively transformed into a dimension of freedom by the parallel evolution of these two powers: to move about, and to perceive at a distance. (Jonas 1966, p. 100).

In his view, only by free moving and perceiving at a distance, most notably by vision, is "space really disclosed to life." The key issue is that (aspects of) the global spatial structure of the environment must become a feature that is present and accessible for an organism. A fly, for example, is able to orient itself within its environment and home in on places with sweet stuff, while avoiding swapping hands. Animals are sensitive to the spatial layout of the environment, for example in the form of patterns on a sensory surface like the retina or the skin, and their behavior is globally organized as a unit in relation to this layout. Barandiaran uses the nice phrase of being sensitive to the "geometric space where objects can be freely explored" (2008, p.198). Such sensitivity comes in different grades, as the fly will not be sensitive to the highly relevant fact for me that it is trying to land on my child's birthday cake.

[4] For Jonas (1966), motility and perception are also intrinsically linked to emotion and the presence of an inner, phenomenal dimension. We will not discuss these further complexities here.

However, in both cases, the fly and me are sensitive or 'aware,' that of the environment as a spatially and temporally extended structure in which we can act.

In contrast, plants are presumed to act on local stimuli, which may guide its behavior in globally appropriate ways, but without being directly sensitive to the spatial patterning of the environment. Thus, plants may grow their roots systematically downward strictly based on the locally available perception of gravity in every root. In this way, they can exploit this geometric structure without being sensitive as a single unit to geometric space as induced by free motility. The issue is the extent to which plants are sensitive to and acting on such global spatial structure of the environment. Or do they get by on the basis of a multitude of local interactions or decision making processes? Thus, the important challenge that Jonas brings forward here for plant cognition is that only free motility seems to bring forth an independent world – a geometric space – in which an agent can act.

Importantly, Jonas shifts the issue from a general unspecific commitment to a sensorimotor organization that plants just do not have, to different, more specific demands that require empirical data to settle. In line with constraint 3, Jonas changes the issue from having an animal-like sensorimotor organization to motility and possible differences in the speed, variability and reversibility of motility. As we will see, recent developments in plant science provide good empirical reasons to downplay the differences between being free-moving and self-induced motility, as imposed by constraint 3. Similarly, sensitivity to the geometric lay out of the environment as stressed by Jonas, may be something that plants are quite capable of without us knowing it. Thus, plants could also very well fulfill constraint 5, making this also an empirical issue rather than a theoretical one.

Constraint 4 stresses the importance of offline control as a way to expand the options of an online operating control structure. Offline control is often considered as a very important sign of cognition. Offline control allows an organism to dissociate its behavior from the immediately impinging stimuli and to act in ways that are guided by forms of knowledge. It is ironic then that these more cognitive offline aspects can be comparatively easy established in plants, when compared to the motility issue.

In the following three sections, we will turn to plant science and discuss developments and examples that make it plausible that plants can fulfill constraints 1 to 5 to some degree, and thus can be deemed cognitive in a sense that is regularly used within *Embodied Cognition*. In particular, the development of plant neurobiology has been important in establishing many details of plant intelligence.

13.6 Plant neurobiology: Intelligence can take different forms and speeds

Plant neurobiology (Baluška et al. 2006) has emerged in the last few years out of the integration of results from areas of research such as plant electrophysiology, cell biology, molecular biology, and ecology. The difference between plant neurobiology and other more basic disciplines resides in the target of these interdisciplinary efforts. Plant neurobiology adds up a scientific understanding of the integration of plant sensing and responding. The target is the scientific understanding of how metabolism and growth can be regulated by the endogenous integration and processing of information. More specifically, plant neurobiology lays the stress on integrated signaling and electrophysiological properties of plant networks of cells. As Baluška et al. (2006) point out:

> "Each root apex is proposed to harbor brain-like units of the nervous system of plants. The number of root apices in the plant body is high, and all "brain units" are interconnected via vascular strands (plant neurons) with their polarly-transported auxin (plant neurotransmitter), to form a serial (parallel) neuronal system of plants." (p. 28).

The working hypothesis of plant neurobiology is that the integration and transmission of information at the plant level involves neuro-like processes such as action potentials, long-distance electrical signaling, and vesicle-mediated transport of (neurotransmitter-like) auxin (Brenner et al. 2006).

Interestingly, from the point of view of the study of plants *qua* information-processing systems, the issue of plant intelligence is less mysterious, or at least subject to investigation in the very same way that cognitive neuroscience deals with in its respective target domain. As recent research in plant neurobiology shows, plants are not passive systems that build up photosynthate. Plants exhibit sophisticated forms of behavior, being able to assess current data that can suppose an advantage at a later stage. Roots, for instance, exhibit patterns of growth that depend upon future acquisition of minerals and water. Plants are indeed sensitive to a minimum of 15 biotic and abiotic signals, among which are not only water, light, minerals, or gravity, but also soil structure, neighbor competition, herbivory, allelopathy, and wind, to name but a few (Trewavas 2000). Likewise, plant roots can, for instance, sense volume, discriminate self from alien non-self roots, and allow for phenotypic root reordering as a function of competition for nutrients. Thus, current evidence easily shows that plant behavior is not at all predefined, as Jonas claimed, but highly variable.[5]

The commonalities in variability of the behavioral repertoires of animals and plants can be strengthened when their different functional and architectural setups are taken into account. The first thing to note concerning plants is that the architectural constraints on cognition may be pretty minimal. When Darwin took the Venus' flytrap as a clear example of a plant with "animal" features (1875), he was not searching for brains in plant's root tips, even though they clearly exhibit sophisticated forms of computation. Darwin (1880) concluded: "…the tip of the root acts like the brain of one of the lower animals, the brain being seated within the anterior end of the body receiving impressions from the sense organs and directing the several movements" (p. 573). As Darwin observed, plant forms of behavior can be highly sophisticated.

Second, although perception, memory and action are capacities that can be present in both animals and plants, they take different forms. Animals, insofar as they are heterotrophic organisms that require organic foodstuff to survive, exploit a number of mobility-related competencies in order to navigate in complex and contingent environments (Neumann 2006). Animals also appear to be better fitted to escape from predators or harmful environments. Plants, by contrast, do not require contractile muscles for fast responses to environmental contingencies. Insofar as plants are autotrophic organisms, they operate in slower time scales since inorganic substrates can be synthesized into organic compounds while remaining stationary. This also means that the computational solutions found by both plants and animals can diverge even when they exhibit similar complex functions.

Someone may nevertheless argue that at the level of the architecture a borderline should be drawn between the two kingdoms. Animal neural networks allow for intelligent behavior courtesy of a hardware arranged in *parallel* (Rumelhart et al. 1986), as opposed to a serial one. However, in our view, it would be a mistake to demand the same type of computational architecture in plants and animals to accommodate constraints 3 and 4. Different architectures can serve to approximate the same function. Non-linearly separable functions may be computed, for instance, by inserting a layer of processing units in between the sensory and the motor layers. In this way, the metric relations of sensory similarity get recoded in terms of functional relations that allow for the approximation of the sensorimotor function, as the logical operation of exclusive disjunction (aka *the XOR problem*) has taught cognitive scientists. But there are many different ways in which a non-linearly separable function can be computed, and inserting a layer in between is not a prerequisite. A two-layer network can equally approximate the function, simply by choosing the right sort of activation function for the problem at hand, such as the cosine or sine transfer

[5] For more sophisticated plant competencies, see Trewavas, 2005.

functions for solving the XOR problem (Rosen et al. 1990). The bearing upon our current concern is thus that in order for plants to exhibit sophisticated forms of computation, a parallel operating neural network may not be necessary.

Thus, differences in speed and architecture have fostered the idea that plant behavior, compared to animal behavior, is strictly determinate and invariant under a variety of conditions. But animal and plant avoidance responses are both graded as a function of the stimulus strength and involve equally modifications in cellular morphology. Plant behavioral invariance is in the eye of the anthropocentric - or *heterotrophicentric*, we may say - observer. But, once we approach the study of (minimal) cognition non-anthropocentrically, perception, memory, and action are common currency across phylogeny.

Summing up, differences in speed and form do not serve to exclude a cognitive interpretation of plant behavior. In our view, the issue is not whether plants can move about, acting intelligently in this way, but rather whether plants, being autotrophic organisms, integrate information, have memory, can make decisions, in such a way that their adaptive coupling to their environment can be called 'cognitive'. Light, gravity, moisture, and touch are signals that plants integrate and respond to in complex non-linear ways. Roots make decisions in particular contexts as to which type of signal(s) to honor (Li & Zhang, 2008). Furthermore, phenotypic plasticity in ever-changing environments requires the exploitation of memory resources. Plants integrate exogenous and endogenous information channels in an attempt to phenotypically adapt to environmental contingencies; a sophisticated form of competency that, we believe, can be paralleled to animals' predictive behavior. In the remainder of this chapter, we are further highlighting the similarities between plant growth and animal memory, and try to show why the behavior of plants, as they are coupled to their environment, allows for a cognitive interpretation of their adaptive responses.

13. 7 Similarities between growth and memory

Take carnivorous *D. muscipula* and *A. vesiculosa*. In the case of *D. muscipula*, an action potential (AP) is generated whenever an upper trap hair is bent. Crucially, a single stimulation of the hair does not trigger the closing of the trap. For the trap to close it is necessary a second AP that takes place only when another hair is bent within 40 secs after the first AP has been generated (Baluška et al. 2006). This setup forms a basic form of memory, similar to the TCST system in bacteria (di Primio et al. 2000) as well as basic forms of animal memory.

Or consider plant's avoidance responses in relation to drought (Trewavas 2003). Drought avoidance behavior results in a reduction in the rate of cell growth that involves, on the one hand, changes in cytosolic Ca^{2+}, $[Ca^{2+}]_i$, and in other second messengers, and, on the other hand, phosphorylation changes in ATPases and associated ion channels related to turgor (Palmgren 2001). Trewavas (2003) compares drought avoidance responses in plants with the avoidance behavior of *Aplysia*. The pattern of avoidance of this marine slug involves a form of short-term memory whose mechanism includes Ca^{2+} and, in addition to the second messengers, cyclic nucleotides and several protein kinases that operate as a temporary memory (Greengard 2001) by phosphorylating ion channels.

Phenotypic plasticity underlies the capability to memorize. Genesis of dendrites delivers the goods in animal brains by effectively altering the architectural features of the network. Different patterns of connectivity permit the network to acquire new functions. Plant networks cannot exploit phenotypic plasticity with the computational resources of animal networks. For one thing, plants' lack neuron-like cells as computational building blocks where new dendrites allow for new functional profiles overall. However, by contrast, plant cell divisions continue at any stage of development. This means that the way to acquire different functionalities throughout the life of the plant will need to differ in architectural terms somehow. Fortunately, as we saw earlier, this need not be an insurmountable hurdle since intelligence is not to be univocally

linked to a specific type of architecture. Trewavas (2003) points out where the architectural divergence may lie: "Just as the process of learning in a brain could be represented as a time series, a set of snapshots of developing brain connections, in plants, each snapshot may possibly be represented by developing plasmodesmatal connections or equally, successive new tissues. So, instead of changing dendrite connections, plants form new networks by creating new tissues, a series of developing brains as it were" (p. 14). In this view, modifying patterns of connectivity is not what allows the plant network to remain competent. Rather, as new tissue accumulates, new networks with different computational resources are stored on top of each other. But note that newer tissue networks do not replace former ones. Rather, we have a succession of operative serial networks, obtained as cells keep dividing throughout the life of the plant.

The key issue in settling upon a non-biased approach to intelligence, as Trewavas (2003) points out, resides in the "delays in the transfer of information between the sensory system and the motor tissues acting upon the signals" (p. 1). But note that these delays cancel out a rendering of plant forms of memory with some class of developmental progression, where previous cellular states determine *linearly* future outcomes (Firn 2004). As Bose and Karmakar (2003) point out, animal neuronal networks and plant calcium signaling systems are not that different in terms of non-linearities. In the case of plants, non-linearities obtain by means of the succession of signaling networks. Chakrabarti and Dutta (2003) have put forward an electrical network that models plant calcium signaling systems and approximates Boolean functions, including XOR. Open/closed ion channels play the role of neurons in networks of plants. As calcium ions are released, diffusion across nearby channels gives rise to further calcium release, ultimately giving rise to a calcium wave that flows throughout the whole network. Such a modeling of calcium signaling networks, Bose and Karmakar (2003) argue, illustrates how memory mechanisms can be implemented in plants. The dynamics of the calcium wave are governed by non-linear equations, opening up the possibility to integrate and compute all incoming data (Trewavas, 2002) in a way that functionally resembles animal-based computation.

If animal memory is characterized by processes that are not linear, the same goes for plants. For a case in point of transfer delay in sensorimotor terms, consider the orchestrated behavior of roots and shoots. Here, there is genuine emergent behavior that cannot be accounted for by summing the local behavior of roots and shoots. Put bluntly, root-shoot interactions can only be understood synergistically (Corning 2003). Or, to put it in computational terms, the XOR function exemplifies the basis of complex behavior insofar as it exploits the delays in the transfer of information between sensory and motor processing tissues, as the metric relations in sensory space are altered in order for the problem to be approximated. We thus have the means to overcome sensorimotor organization as a restriction (constraint 3, above). In what follows, we illustrate from a behavioral perspective how plants have offline capabilities (constraint 4) that allow them to do more than reacting to immediate stimuli.

13.8 Offline cognition: Leaf heliotropism

Someone may argue that the issue is not whether the function to be computed is linearly or non-linearly separable, embodied or not, but rather whether the recoding of the metric relations that obtain as a result of the approximation of the function can be interpreted in representational terms. In other words, the issue is whether plants, however complex calcium wave networks happen to be, manipulate representational states or not. Take the case of the stilt palm. In order to avoid competition for light, the stilt palm (Allen 1977) "walks" away from shade and into sunlight. The stilt palm grows new roots in the direction of sunlight, allowing older roots to die. Although Trewavas (2003) interprets this as an *intentional* form of light-foraging behavior, it is usually assumed that de-coupled, offline modeling tasks are what distinguish sophisticated forms of

behavior from merely tropistic online routines. Put bluntly, the *sine qua non* of representation-based competency is offline adaptive behavior (Clark, 1997).

Generally speaking, tropisms involve a directional change such as growth or movement in response to a given environmental stimulation (Stanton and Galen 1993). Nevertheless, plant tropisms can vary substantially as a function of the type of stimulus that the plant is responsive to, and the part of the plant that responds to the stimulation. Complex, although still online, tropistic reactions are frequent. Roots that manifest gravitropism stop developing downwards as they encounter a physical obstacle, and grow horizontally instead. However, they are able to assess online the state of affairs, and periodically try to move downwards, remaining horizontal if unable to respond gravitropically (see Massa and Gilroy 2003). Likewise, we may think of thigmotropism, hydrotropism, or thermotropism, as other sophisticated, although possibly, still online, tropistic responses.

But some plant tropisms do constitute a form of offline anticipatory behavior. In relation to light-related tropisms, we can distinguish phototropisms, which may represent directed responses to a static light source, from heliotropism, a more complex response that involves a correlated response to changes in sunlight orientation as the day changes from sunrise to sunset. We may also differentiate between flower heliotropism and leaf heliotropism. In the case of flower heliotropism, no "memory" mechanisms seem to be required for flowers to keep track of the position of the sun. Unless flowers are exposed to light in the morning they will fail to reorient to sunrise, remaining in a random orientation throughout the night.

But offline nocturnal reorientation by plant leaves represents a qualitative change with regard to stimulus controlled online behavior. Leaf laminas of *Lavatera cretica* can, not only anticipate the direction of the sunrise, but also allow for this anticipatory behavior to be retained for a number of days in the absence of solar-tracking. That is, the laminas reorient during the night and keep facing the direction of the sunrise even after a few days without tracking the sun, and without sensing the position of sunset. Schwartz and Koller (1986) report a series of experiments that clearly shows that this is a complex offline response. Three groups of plants were taken at sunset to 3 different cabinets. One was kept in darkness; another had illumination in day-light hours, and another one was kept illuminated vertically throughout the experiment. The first day, plants in cabinets 1 and 2 (darkness and day-light hours conditions) could anticipate sunrise and leaves were oriented towards that direction. Plants in cabinet 3, on the other hand, were horizontal, with laminas facing upwards, as they had been kept under constant vertical artificial illumination. The nocturnal reorientation behavior exhibited by plants in cabinets 1 and 2 lasted for as long as 3 days under the same experimental conditions, that is, in the absence of day-time solar-tracking. In their study, the explanation of nocturnal reorientation cannot be the sunrise of the day before, since plants were prevented from tracking the sun for 3-4 days.

The explanation of nocturnal reorientation involves the internal modeling of environmental rhythms. Circadian clocks allow for time-estimation by synchronizing endogenously generated activity with exogenous cyclic periods such as day-night planetary patterns. Circadian clocks can mimic biological rhythms on a 24-hour cycle, and this explains nocturnal reorientation in plants for up to 4 days in the absence of sunrise stimulation. Plant genetics points towards underlying shared molecular components that explain day-length estimations and the operation of light receptors (see Pruitt et al. 2003, and references therein). In the case of time-estimation, recent research in genomics has unearthed the molecular mechanisms of plant overt behavior, with the result that both plants and animals draw on the very same molecular networks (Cashmore 2003) in their adaptive exploitation of circadian clocks. One single level, thus, explains the origins of the anticipatory behavior as exemplified by circadian clocks.

As we saw earlier, the type of restrictions imposed by constraints 3 and 4 serve to stress the importance of having a sensorimotor organization, on the one hand, and improving the offline and information processing capacities of the system, on the other. Offline plant behavior may thus

be considered minimally cognitive insofar as information is processed flexibly and adaptively in accordance with the aforementioned restraints. Constraint 5, nonetheless, remains an open empirical question, although there are reasons to be optimistic, as we point out in the closing section.

13.9 Concluding remarks

The notion of cognition is very much in flux. Within *Embodied Cognition* the meaning of cognition has been changed from human thought to a broader interpretation centered on perception and action. In this perspective, free-moving animals are part of the cognitive domain but sessile plants, without clear perception and action features and a dedicated sensorimotor organization, form a more difficult case. Given that plants are definitely capable of many forms of complex behavior, they provide an interesting domain for both questioning and clarifying *Embodied Cognition*'s focus on free-moving agents. At the same time, *Embodied Cognition's* wide reading of cognition can reinforce the study of intelligence in plants, as it now occurs within the field of plant neurobiology.

We discussed how *Embodied Cognition* interpreted cognitive phenomena, and summarized this view in terms of five constraints on cognition (Section 5). Two of these constraints (3 and 5) emphasize being free-moving as a definite requirement for minimal forms of cognition. This seems to contradict the possibility of plant cognition. We used an analysis of Hans Jonas to articulate the requirements for being considered 'free-moving' and to assess possible reasons for its importance. Subsequently, we argued that these two constraints should be readjusted, allowing the possibility that plants fulfill these constraints in ways that differ from those in free-moving creatures. We then discussed work in plants sciences to see whether it is plausible that plants can fulfill the five constraints formulated above.

Plants fulfill the first two of these constraints: having a metabolic organization that provides a normative context, and exploiting environmental spatio-temporal structure to enhance metabolic functioning. Our discussion centered on evidence for constraint 3 (sensorimotor organization), 4 (offline control), and 5 (acting as a global unit). Interestingly, while it is relatively easy to establish the presence of offline control in plants, which is generally considered the key notion of cognition, the evidence concerning the role and organization of motility and perception in plants remains more equivocal and difficult to interpret.

There is a large gap between facts and possible interpretations here. New developments in plant neurobiology have made it clear that plants are capable of much more complex behavior than many of us tended to think, including Jonas. We have argued that it is plausible that plants can circumvent the requirement for an animal sensorimotor organization. They are capable of organizing their behavior in ways that are different but still highly complex and adaptive, making this behavior cognitive in the general and minimal sense used within *Embodied Cognition*. It remains to be seen to what extent plants can really fulfill constraint 5. Plants integrate information simultaneously provided by many different sensors on a variety of parameters in real time and it may very well be that this allows them their own equivalent of the sensitivity provided by animal sensory surfaces. We expect that plant neurobiology will clarify this issue further in the near feature given its emphasis and focus on the integration of information present in different parts of the plant.

Concluding, we hope to have shown that, in a number of specific issues relating to cognition, animals and plants do not fundamentally differ, and plants are cognitive in a minimal, embodied sense that also applies to many animals and even bacteria. The scientific target in both cases is to understand the continuous interplay of animals and plants in relation to the environmental contingencies that impinge upon them. Plant cognition is in this view not a contradiction at all but an empirical issue that requires much more attention, not only from plant scientists but also from cognitive scientists, more generally.

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